

## Protective Display and Sound Production in Some New World Arctiid and Ctenuchid Moths<sup>1</sup>

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(Text-figures 1-29)

### 1. INTRODUCTION

**D**ESPITE a large literature on the protective devices of arthropods, there have been few attempts to study their evolution within restricted taxa in relation to particular natural communities. Such studies are to be desired because the growth of knowledge about the behavior of predators in prey/predator situations (see reviews by de Ruiter, 1956; Sheppard, 1959, 1961) has led to a belief that the selection pressures which determine the evolution of protective behavior may be formulable in fairly simple terms, and that the end-products of evolution under given circumstances may be to some extent predictable. For instance, a discussion of Müllerian and Batesian mimicry based on assumptions of this type has been given by Huheey (1961), and of the constraints which may modify the adult lifespans of some hemileucine saturniid moths by Blest (1963b).

Nevertheless, it may be doubted whether many natural situations present a sufficient degree of simplicity for such analyses, and the present more superficial survey of a large fauna may serve to illustrate some of the difficulties of such an approach.

The protective display behavior of arctiid and ctenuchid moths will be described in three main neotropical locations: at Barro Colorado Island, in the Panamá Canal Zone (lowland seasonal

tropical evergreen forest: Bennett, 1963); at Volcán and Santa Clara near the Panamá-Costa Rica border (seasonal lower montane forest at 4,000-5,000 ft. above sea level); and in the Arima valley of Trinidad (transitional between lower montane rain forest and lowland seasonal forest, at an effective altitude of 500-1,800 ft. above sea-level (Beard, 1946; Beebe, 1952).

These two families were chosen because they form a group of allied, numerous and predominantly distasteful species, a large proportion of which have been accessibly monographed for the areas concerned (Forbes, 1939; Kay & Lamont, 1937; Fleming, 1957, 1959).

The nomenclature follows that used in the current arrangement of material in the British Museum (Natural History) collections, and it may be noted that Forbes (1939) lists illustrations in Seitz (1915-17) for most of the species which he records for Barro Colorado and comments on their accuracy.

Although the ctenuchid fauna is a rich one, this group has not been studied in as much detail as the arctiids; a sufficient range of species has been examined to establish the general behavioral continuity between the two families, which also show a wide range of morphologically transitional forms (Forbes, 1939). The use of light traps to secure material has caused the predominantly diurnal Ctenuchinae to be poorly represented. No attempt has been made to study the behavior of the minute and fragile lithosiine arctiids. The behavior of virtually all the dominant species on Barro Colorado has been examined between May 5-September 20, 1961, July 2-September 20, 1962, and the month of July, 1963; only those species which are rare or whose identity is uncertain are omitted. In Trinidad, only the most common species were seen

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in April, 1961, and work at Volcán and Santa Clara was confined to three weeks in July, 1961.

## 2. MATERIALS AND METHODS

The moths were captured as adults at light traps which were run throughout the night; the insects were removed from the vicinity of the light and placed in separate containers as soon as possible after arrival at the traps. The simple methods for examining protective display behavior have been described elsewhere (Blest, 1957).

The palatability tests employed White-faced Monkeys, (*Cebus albifrons*), and Geoffroy's Pinché (*Oedipomidas spix*) (Canal Zone); and domestic fowl (Santa Clara). The monkeys and marmosets were confined in groups of 4-6 in large outdoor cages.

## 3. MODES OF PROTECTIVE BEHAVIOR

The protective devices can be divided into a small number of behavior patterns found widely throughout the two groups, while occasionally showing marked taxonomic segregation, and a larger number of specialized devices with a much more scattered distribution, usually combined in some way with the basic display types. The behavioral repertoire may be summarized as follows:

I. *The Emission of Ultrasonic Signals.*—One species, *Melese laodamia*, has been shown to emit ultrasonic sounds at high intensity when it is roughly handled; the presence of the sound-producing organs on other species, and the emission by them of sounds with a faint audible component, allowed the assumption that they too are primarily generating noises in the ultrasonic range (Blest, Collett & Pye, 1963) and recent observations have confirmed that they do so. The sounds are produced by modified episternites of the metathorax. Those of *Melese* are modulated between 30 and 90 Kc/sec. Each burst of sound is composed of a train of cycles of modulation which sweep over the main frequency range some forty times/second; the modulation cycles themselves are formed from a series of discrete pulses whose repetition rate may rise to over 1,000/sec. The mechanics and acoustics of the process of sound production are discussed in detail elsewhere, together with their possible function. The latter is, however, quite obscure; the thresholds of sound production to tactile stimulation are very variable, and it is not yet clear what proportion of species will emit them while on the wing, or in what stimulating circumstances (Blest, Collett & Pye, 1963).

Table 1 includes a summary of the thresholds

at which sounds are produced to handling the insects. Species with a low threshold (L) will start to make sounds as soon as they are picked up and held lightly; those with medium thresholds (M) need to be squeezed, or rolled lightly between the fingers; species with high thresholds (H) must be manipulated to the point of mutilation. Those species marked "VH" perform erratically and only a minority of individuals will respond to mutilation. This classification reveals that (a) any mode of protective coloration can be linked to sound production; (b) the advanced mimetic ctenuchids have lost the ability to make sounds; the anatomical condition of the tymbal organs (*i.e.*, their reduction to leathery and densely scaled structures) suggests that they are unlikely to use them in any circumstances; (c) there is within the arctiids, at least, a correlation between threshold of sound production, "toughness," and palatability. This relationship reveals that, predominantly, palatable arctiids have a low threshold for sound emission, while distasteful species are more likely to possess the higher thresholds.

In addition there is another unexplained correlation. While distasteful species with high thresholds for sound production are likely to have their flight periods at any time in the night, palatable species with low thresholds concentrate their flights between 3 and 5 o'clock in the morning. Table 2 summarizes the data for 35 species of arctiid and ctenuchid. The individual moths arriving at an ultra-violet light-trap were recorded hourly and removed from the light and destroyed after they had been scored. The table gives the total number of male individuals for each group of species which were recorded nightly over a three-week period on Barro Colorado Island from June 30-July 25, 1962. It is unlikely that these correlations can be understood until more is known about the emission of ultrasound in free flight, and about the normal flight times of insectivorous bats in the habitats concerned. Several species of arctiid and ctenuchid, including the genera *Melese* and *Halysidota*, can be made to reply with bursts of ultrasound to pulses from a bat simulator (Roeder, unpublished data; Pye, Pye, Flynn & Blest, in prep.), but the significance of this response is not yet understood.

II. *Classical "Reflex Immobilization."*—The use of the term will be restricted, for reasons which have already been discussed (Blest, 1957), to immobilization, or "freezing" which does not involve the assumption of a specialized posture. Characteristically, in both families, it does not outlast actual handling by more than a few seconds, and is given only to a constraining tactile

TABLE 1. LIST OF SPECIES STUDIED, WITH NOTES ON THEIR DISPLAY TYPES, PALATABILITY AND SOUND PRODUCTION

Conventions: Localities: B — Barro Colorado  
 S — Santa Clara and Volcan  
 T — Arima Valley, Trinidad

Display Type: R — Reflex immobilization  
 II — Type II display  
 III — Type III display  
 W — Wing-waving display

Sound Production: L — Low threshold to tactile stimuli  
 M — Moderate " " "  
 H — High " " "  
 VH — Very High " " "

All of the species listed below have been checked against authenticated specimens in the collections of the British Museum (Natural History). Where insufficient specimens were available for valid comparison, or there were no authenticated specimens available, the species is marked †.

ARCTIIDAE PHAEGOPTERINAE (77 species)	Locality	Display type	Additional components, etc.	Sound production	Palatability and notes
<i>Automolis lineosa</i> Walker	B	R	————	L-M	Rejected by <i>Cebus</i>
<i>A. lineatus</i> Druce	B	R	————	L-M	" " "
<i>A. sp.</i> (unidentified) †	S	R	————	—	Near to <i>A. lineatus</i>
<i>A. reducta</i> Walker	B	R	————	H	Rejected by <i>Cebus</i>
<i>A. dilutus</i> Felder	B	R	Falls to visual stimuli or touch	H	" " "
<i>A. pauperis</i> Schaus	S	III	————	—	Rejected by fowls
<i>A. rutila</i> Stoll	BT	III	Text fig. 9	H	Rejected by <i>Cebus</i>
<i>A. priscilla</i> Rothschild	B	III	————	H	One female only
<i>A. chionoplaga</i> Dognin	B	III	Text fig. 10	H	Rejected by <i>Cebus</i>
<i>A. sicilia</i> Druce	BS	III	————	H	" " "
<i>A. metallica</i> Joicey	BT	III	————	H	" " "
<i>A. taeniata</i> Guerin	S	III	Text fig. 11	VH	Rejected by fowl
<i>A. vitrea occidentalis</i> Rothschild	B	III	————	H	Rejected by <i>Cebus</i>
<i>A. vinasia</i> Schaus	S	R	————	(—)	Two specimens only
<i>A. elissa</i> Schaus	B	III	————	H	Rejected by <i>Cebus</i>
<i>A. elissoides</i> Rothschild	B	III	Text figs. 7 & 8	H	" " "
<i>A. salma</i> Druce	B	III	————	?	One male, Aug. 1963
<i>A. crithéis</i> Druce	B	R(III)	————	—	Rejected by <i>Cebus</i>
<i>A. tegyra</i> Druce	BS	III	Text fig. 12	VH	" " "
<i>A. obscurata</i> Schaus	B	R(III)	Cryptic color pattern	L	Palatable
<i>Cissura plumbea</i> Hampson	B	R	————	H	Rejected by <i>Cebus</i>
<i>Prumala sp.</i> †	S	R	————	—	Accepted by fowl. Near <i>P. suanus</i> Druce, and matches unidentified specimens from Volcan in British Museum collection
<i>Idalus hippia</i> Stoll	B	R	————	M	————
<i>I. daga dares</i> Druce	B	R(III)	————	—	Rejected by <i>Cebus</i>
<i>Eupseudosoma aberrans</i> Schaus	B	R(III)	————	L	} Rejected by <i>Cebus</i>
<i>E. aletis</i> Schaus	B	R(III)	————	L	
<i>Robinsonia similis</i> Rothschild	T	III	————	M-H	} —————
<i>R. deiopea</i> Druce	B	III	Text fig. 18	M-H	
<i>R. sanae</i> Druce	B	III	Text fig. 19	M-H	
<i>R. variegata</i> Rothschild	B	III	} Rest with striped abdomen exposed. Convergent to small Pericopidae	M-H	
<i>R. flavomarginata</i> Reich.	B	III			
<i>Baritius hamptoni</i> Dognin	B	II	————	—	} Rejected by <i>Cebus</i>
<i>B. haemorrhoides</i> Schaus	B	II	————	—	
<i>B. superba</i> Schaus	BS	II	Text fig. 2	—	
<i>Pachydota saduca</i> Druce	S	II	} No abdominal component. Text fig. 6	—	} —————
<i>P. affinis</i> Rothschild	T	II			
<i>P. punctata</i> Rothschild	B	II			

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<i>Melese laodamia</i> Druce	BT	R	Text fig. 16	L	<i>M. laodamia</i> rejected by Silver-beaked Tanagers. <i>M. laodamia</i> , <i>M. asana</i> and <i>M. incerta</i> accepted by both primates. <i>M. russata</i> and <i>chiriquensis</i> (1 ♂) accepted by fowl on majority of occasions
<i>M. russata</i> H. Edwards	S	R	————	L	
<i>M. asana</i> Druce	B	R	Forelegs sometimes quivered, as in <i>Bertholdia</i> . Text fig. 15	L	
<i>M. incerta</i> Walker	BT	R		L	
<i>M. chiriquensis</i> Schaus	S	R	————	L	Accepted by fowl
<i>Bertholdia grisescens</i> Rothschild †	S	II	Abdomen not curled forelegs raised and quivered. Text fig. 5	L	
<i>B. myosticta</i> Hampson	S	II		L	Rejected by fowl
<i>B. fumida</i> Schaus	S	II		L	Single specimen
<i>B. albipunctata</i> Schaus	B	II		L	Single specimen
<i>Neritos cotes</i> Druce	B	R	————	M	Accepted by primates
<i>N. suffusa</i> Rothschild	BT	R	————	M'	
<i>Ochrodota pronapides</i> Druce	BS	R	Text fig. 17	L	Accepted by <i>Cebus</i> & fowl
<i>Phaemolis lepida</i> Schaus	B	R	————	L	Accepted by <i>Cebus</i>
<i>Neaxia bella</i> Schaus	B	R	————	L	
<i>Eriostepta beata</i> Dognin	B	R	————	L	
<i>Araeomolis persimilis</i> Rothschild	B	R	————	L	
<i>Amaxia pyga</i> Schaus	B	R	————	H	————
<i>Amaxia chaon</i> Druce	B	R	————	L	
<i>Ammalo helops</i> Cramer	B	R	————	---	Rejected by <i>Cebus</i>
<i>Elysius conspersa</i> Walker	B	R	————	---	
<i>Amastus rumina</i> Druce	S	R	————	---	————
<i>Opharus astur</i> Cramer	BS	R	————	---	————
<i>Psychopasma erosa</i> Herrich-Schaffer	B	R	————	---	————
<i>Castrica phalaenoides</i> Drury	B	R	————	M	————
<i>Tricypha imperialis</i> Heylaerts	B	R	————	---	Rejected by <i>Cebus</i>
<i>Pelochyta misera</i> Schaus	B	R	————	---	————
<i>Halysidota interlineata</i> Walker	B	R	Forelegs raised and quivered as in <i>Bertholdia</i> . Abdomen not curled. The display of <i>H. interlineata</i> infrequent and transient	---	Rejected by <i>Cebus</i>
<i>H. underwoodi</i> Rothschild	S	R-II		---	---
<i>H. atra</i> Druce	S	R-II		---	---
<i>H. cyclozonata</i> Hampshire	B	R	————	L	Accepted by <i>Cebus</i>
<i>H. iridescens</i> Schaus	B	R	————	L	
<i>H. marionensis</i> Schaus	B	R	————	---	
<i>H. angulata</i> Rothschild	B	R	————	---	
<i>Glaucostola guttipalpis</i> Walker	B	R	————	M	————
<i>G. reimana</i> Schaus †	B	R	————	M	————
<i>G. flavida</i> Schaus	B	R	————	M	Rejected by <i>Cebus</i>
<i>G. metaxantha</i> Schaus †	B	R	————	?	One male, July, 1963
<i>Agoraea semivitrea</i> Rothschild	B	II	————	---	————
<i>Metaxanthia aureiventris</i> Rothschild	B	R	————	---	————
<i>M. atribasis</i> Rothschild †	B	R	————	---	Agrees with Forbes's description of specimens from Barro Colorado, but not with authenticated specimens. Possibly a new species.
<b>BELEMNIINAE (3 species)</b>					
<i>Belemnia pavonia</i> Forbes	B	RW	————	---	Rejected by <i>Cebus</i>
<i>Belemniastis troetschi</i> Druce	B	RW	Frothing from thorax	---	
<i>Diospage chrysobasis</i> Hampson	B	RW	" "	---	————

TABLE 1. LIST OF SPECIES STUDIED, WITH NOTES ON THEIR DISPLAY TYPES, PALATABILITY AND SOUND PRODUCTION (CONTINUED)

ARCTIIDAE ARCTIINAE (5 species)	Locality	Display type	Additional components, etc.	Sound production	Palatability and notes
<i>Epantheria laeta</i> Walker	B	II	—	—	} Rejected by <i>Cebus</i>
<i>E. muzina</i> Oberthür	T	II	Text fig. 3	—	
<i>E. icasia trinitatis</i> Rothschild	B	II	—	—	} Rejected by <i>Cebus</i>
<i>E. orsa</i> Cramer	B	II	—	—	
<i>Virbia rosenbergi</i> Rothschild	B	II,W	Some slow elevation and depression of the wings	—	Accepted by <i>Cebus</i>
CTENUCHIDAE					
EUCHROMIINAE (35 species)					
<i>Histaeta cepheus</i> Cramer	T	RW	Copious reflex bleeding	VH	Sounds made by single male only
<i>Homoeocera stictosoma</i> Druce	B	RW	Male with ventral valve secretion	—	Rejected by <i>Cebus</i>
<i>Autochloris jansonis</i> Butler	B	RW	Frothing of pericopid type	—	Rejected by <i>Cebus</i>
<i>Sarosa innotata</i> Draudt	B	RW	"Bobbing" of abdomen	—	Rejected by <i>Cebus</i>
<i>Gymnelia salvini</i> Butler	B	RW	—	—	" " "
<i>Phoenicoprocta paucipuncta</i> Dyar	B	RW	—	—	" " "
<i>P. vacillans</i> Walker	T	RW	—	—	
<i>P. insperata</i> Walker	B	RW	—	—	
<i>Mesothera pyrrha</i> Schaus	B	RW	—	—	
<i>Cosmosoma teuthras</i> Walker	B	RW	—	—	Rejected by <i>Cebus</i>
<i>C. batesi</i> Butler	B	RW	—	—	—
<i>C. hercyna hercynacula</i> Dyar	B	RW	—	—	
<i>C. metallescens</i> Menetries	B	RW	—	—	
<i>C. remotum</i> Walker	B	RW	—	—	
<i>C. advena</i> Druce	S	RW	—	—	
<i>C. klagesi</i> Rothschild	T	RW	—	—	
<i>C. metathoracica</i> Kaye	T	RW	—	—	
<i>C. bogotensis</i> Feld	B	RW	—	—	One male only
<i>Saurita clusia</i> Druce	BT	RW	—	—	} Rejected by <i>Cebus</i>
<i>S. afflicta</i> Walker	BT	RW	—	—	
<i>S. anselma</i> Schaus	B	RW	—	—	
<i>Isanthrene crabroniformis</i> Staudinger	S	II	Very wasp-like in flight. Text fig. 4	—	One female only
<i>Psoloptera thoracica</i> Walker	B	RW	—	—	Rejected by <i>Cebus</i>
<i>Rhynchopyga cryptoleuca</i> Walker	B	RW	—	—	" " "
<i>Dycladia vitrina</i> Rothschild	B	R	—	—	
<i>Phoenarete diana</i> Druce	S	II-W	Display posture assymetrical	—	Rejected by chickens
<i>Macrocneme adonis</i> Druce	B	RW	} Male genitalia extruded. Text fig. 1a	—	All <i>Macrocneme</i> tested with <i>Cebus</i> were rejected
<i>M. thyra</i> Moschler	BT	RW		—	
<i>M. cyllarus</i> Druce	B	RW		—	
<i>M. hampsoni</i> Schrottky	B	RW		—	
<i>M. auripes</i> Walker	B	RW		—	
<i>M. chrysotarsia</i> Hampson	B	RW	—		
<i>Calonotos tiburtus</i> Cramer	B	RW	} Male genitalia extruded. Text fig. 1a	—	} Rejected by <i>Cebus</i>
<i>C. metallicus</i> Druce	B	RW		—	
<i>C. craneae</i> Fleming	T	TW		—	

TABLE 1. LIST OF SPECIES STUDIED, WITH NOTES ON THEIR DISPLAY TYPES, PALATABILITY AND SOUND PRODUCTION (CONTINUED)

CTENUCHIDAE CTENUCHINAE (63 species)	Locality	Display type	Additional components, etc.	Sound production	Palatability -and notes
<i>Marecidia achrysa</i> Forbes †	B	RW	-----	---	Rejected by <i>Cebus</i>
<i>Eumenogaster moza</i> Druce	B	RW	-----	---	" " "
<i>Chrysostola fulvisphex</i> Druce	B	RW	-----	---	
<i>Pterygoterus leucomela</i> Walker	B	RW	-----	---	Mimics general facies of sphecid wasp. Antennae palpate ground when walking, and movement jerky. Rejected by <i>Cebus</i>
<i>Androcharta meones</i> Stollinger	B	RW	-----	---	-----
<i>Amycles anthracina</i> Walker	B	RW	-----	---	
<i>Atyphopsis modesta</i> Butler	B	R	-----	---	
<i>Episcepsis venata</i> Butler	B	R	-----	---	Certain of these very similar species producesounds when they are handled roughly (M), but the distribution of sound production has not been studied. All are superficially much alike, and all those tested were rejected by <i>Cebus</i> . Single specimens from Barro Colorado, tentatively assigned to <i>E. vinasia</i> Schaus, <i>E. klagesi</i> Rothschild and <i>E. demonis</i> Druce have also been taken.
<i>E. lamia</i> Butler	B	R	-----	---	
<i>E. lenaeus</i> Cramer	B	R	-----	---	
<i>E. hypoleuca</i> Hampson	B	R	-----	---	
<i>E. frances</i> Dyar	B	R	-----	---	
<i>E. gnomoides</i> Schaus	B	R	-----	---	
<i>E. capysca</i> Schaus	B	R	-----	---	
<i>E. pseudothetis</i> Fleming	T	R	-----	---	
<i>E. redunda</i> Schaus	T	R	-----	---	
<i>Eucereon aoris</i> Moschler	B	R	-----	L	
<i>E. aeolum</i> Hampson	B	R	-----	L	
<i>E. obscurum</i> Moschler	B	R	Specialized resting posture. Text fig. 14	L	
<i>E. leria</i> Druce	S	R	Crimson cervical hairtufts. Text figs. 20, 21	M	
<i>E. tarona</i> Hampson	B	R		M	
<i>E. formosa</i> Dognin	S	R	Text fig. 27	M	
<i>E. atrigutta</i> Druce	B,S	R	-----	M	
<i>E. venosa</i> Schaus	B	R	-----	M	
<i>E. rosa</i> Walker	B	R	-----	H	
<i>E. maia</i> Druce	B,T	R	Text fig. 29	H	
<i>E. zamorae</i> Dognin	B	R	-----	---	
<i>E. flavicaput</i> Hampson	B,S	R	Text fig. 24	---	
<i>E. scyton</i> Cramer	B	R	-----	---	
<i>E. decora</i> Schaus	S	R	Dorsal abdominal hair tufts	---	
<i>E. xanthura</i> Schaus	B	R	-----	---	
<i>E. intranotata</i>	B	R	-----	---	
<i>E. myrtusa</i> Druce	S	R	-----	---	
<i>E. latefascia</i> Walker	B	R	Text fig. 22	---	
<i>E. pseudarchias</i> Hampson	B	R	-----	---	
<i>E. striata</i> Druce	S	R	-----	---	
<i>E. rogersi</i> Druce	B,S	R	Text fig. 25	---	
<i>E. tigrata</i> Herrich-Schaffer	S	R	Text fig. 26	---	
<i>E. costulata</i> Herrich-Schaffer	S	R	Text fig. 28	---	
<i>E. zephyrus</i> Schaus	B	R	-----	---	
<i>Heliura balia</i> Hampson	B	R	Text fig. 23	---	
<i>H. rhodophila</i> Walker †	B	R	-----	---	

TABLE 1. LIST OF SPECIES STUDIED, WITH NOTES ON THEIR DISPLAY TYPES, PALATABILITY AND SOUND PRODUCTION (CONTINUED)

CTENUCHIDAE CTENUCHINAE (63 species)	Locality	Display type	Additional components, etc.	Sound production	Palatability and notes
<i>H. banoca</i> Forbes †	B	R	————	—	All <i>Heliura</i> and <i>Delphyre</i> rejected by <i>Cebus</i>
<i>Delphyre rubricincta</i> Hampson	B	R	Foul odor released when handled	—	
<i>D. atava</i> Druce	B	R	Resembles <i>Episcepsis</i>	ML	
<i>D. aurorina</i> Forbes †	B	R	————	—	
<i>Correbia lycoides</i> Walker	BT	R	Very heavily sclerotized	—	All are lycid beetle mimics, and all are rejected by <i>Cebus</i>
<i>C. affinis</i> Druce	B	R	————	—	
<i>Correbidia terminalis</i> Walker	BT	R	Weakly sclerotized	—	
<i>Hyaleucera luctuosa</i> Moschler	B	R-II	————	—	————
<i>H. fusiformis</i> Walker	B	R-II	————	—	————
<i>H. gigantea</i> Schaus	BS	R	Resting posture and behavior like <i>Eucereon obscurum</i>	—	————
<i>Ptychotrichos zeus</i> Schaus	B	II	Abdomen curled, wings not elevated	—	————
<i>Napata walkeri</i> Druce	BT	R	All are tough and bear bold patterns when they are at rest	L	All are rejected by <i>Cebus</i>
<i>N. leucotelus</i> Butler	B	R		L	
<i>Aclytia gynamorpha</i> Hampson	B	R		L	
<i>A. punctata</i> Butler	B	R		L	
<i>A. albistriga</i> Schaus †	B	R		L	
<i>Leucopleura ciarana</i> Schaus †	B	RW	Genitalia extruded by both sexes	—	Rejected by <i>Cebus</i>
<i>Xanthopleura troetschi</i> Druce	B	RW	————	—	————

stimulus. It may be associated with other, more specialized, postures, for example, the extrusion of colored genital processes, of colored tubes from the cervical region, or of abdominal hair tufts (see below). This is the typical protective response of the ctenuchids, and two examples are given in Text-fig. 1.

III. *Wing-waving Displays*.—The wings, which are protracted from rest, are slowly and gently elevated and depressed. These displays are similar to the saturniid rhythmic displays (Types III & IV) (Blest, 1957). They are found in the North American *Diacrisia virgo*, in virtually all the mimetic Ctenuchidae as a concomitant of walking, and in *Virbia* spp. following Type II display. Transitional genera between the Arctiidae and Ctenuchidae (e.g., *Belemnina*, *Belemnistis* and *Diospage*, but not *Metaxanthia*) also wave their wings as they walk.

IV. *Type II Sustained Static Displays*.—These have been described for the hemileucine Saturniidae (Blest, 1957). The moth falls from its substrate, curls the abdomen so that the dorsal surface is convex, and places its legs in a characteristic posture; the wings are simultaneously elevated (Text-figs. 2-6). Static displays of this kind may

be maintained for periods of a few seconds up to several minutes by saturniids such as *Dirphia* (*Periphoba*) *hircia* (Blest, 1960). Among the present families these displays show more variety: the abdomen is not always curled, and the angle of wing elevation and leg-extension varies widely between species.

V. *Type III Sustained Static Displays*.—Displays of this type are the converse of the Type II displays; the abdomen is elevated instead of depressed, so that it projects above the folded wings at right angles to the substrate, and the wings are slightly depressed. The abdomen itself is usually bright colored and banded (Text-figs. 7-12).

#### VI. *Special Devices*:

(i) *Extrusion of the Male Genitalia*.—The male genital processes may be ornamented with brightly-colored tufts of hair (e.g., *Baritius haemorrhoides*), or they may be so feebly sclerotized that they assume the color of the blood (e.g., *Macrocne me thyra intacta*, *Calonotos craneae*). In species so decorated the genitalia are extruded during display (Text-fig. 1).

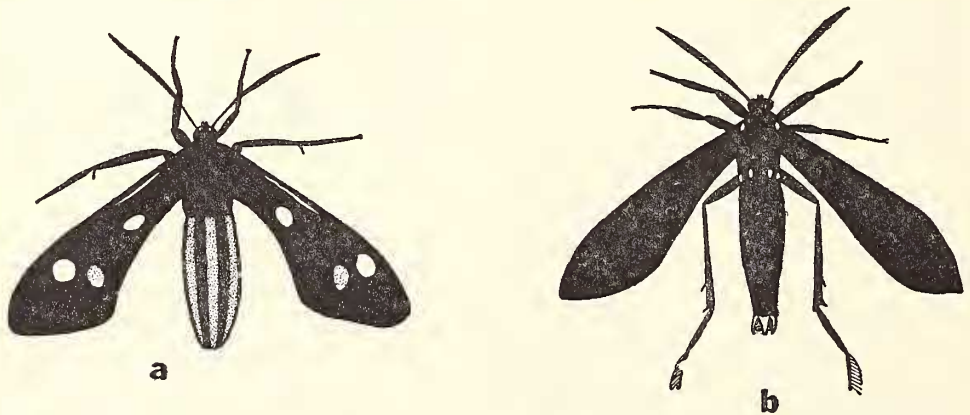
(ii) *The Display of Abdominal or Cervical*

TABLE 2. FREQUENCY WITH WHICH MALE MOTHS WERE CAPTURED AT HOURLY INTERVALS THROUGHOUT THE NIGHT OVER A THREE-WEEKS PERIOD (JUNE 30–JULY 25, 1962), ON BARRO COLORADO ISLAND

I. ARCTIIDAE Flight Times Species	19:00- 20:00	20:00- 21:00	21:00- 22:00	22:00- 23:00	23:00- 24:00	24:00- 01:00	01:00- 02:00	02:00- 03:00	03:00- 04:00	04:00- 05:00	Totals	Sound Threshold
	<i>Melese laodamia</i>	3	1	1	0	1	3	0	1	118		
<i>M. incerta</i>	1	2	2	3	1	4	8	33	60	20	134	L
<i>M. asana</i>	1	0	1	0	3	0	0	0	2	2	9	L
All <i>Melese</i>	5	3	4	3	5	7	8	34	180	41		
<i>Automolis obscurata</i>	1	3	0	0	1	0	0	1	4	13	22	L
<i>Halysidota iridescens</i>	0	1	0	0	0	0	1	5	15	7	29	L
<i>Automolis dilutus</i>	1	1	17	20	4	2	0	0	1	1	47	H
<i>A. critheis</i>	0	3	7	5	0	1	0	0	0	0	16	Silent
<i>A. rutila/A. chionoplaga</i>	2	3	0	0	0	0	0	1	0	0	6	H
<i>A. elissa/A. elissoides</i>	0	0	0	0	0	0	3	0	0	0	3	H
<i>A. sicilia/A. metallica</i>	1	1	1	0	3	2	2	0	0	0	10	H
<i>A. lineosa</i>	0	0	1	4	2	0	1	0	1	0	9	L-M
All <i>Automolis</i>	4	8	26	29	9	5	6	1	2	1		
<i>Robinsonia variegata/ R. sanae/R. deiopea</i>	1	0	1	2	2	0	2	0	0	1	9	M-H
<i>Amaxia pyga</i>	1	0	0	2	2	10	5	3	2	0	24	H
<i>Elysius conspersa</i>	0	0	0	3	10	5	2	1	0	0	21	Silent
II. CTENUCHIDAE												
<i>Eucereon pseudarchas</i>	0	3	3	6	4	3	3	0	4	0	26	Silent
<i>Aclytia gynamorpha</i>	3	9	6	2	0	0	2	0	0	2	24	L
<i>Episcepsis</i> spp.	3	13	6	6	3	2	3	0	2	2	40	M-silent
<i>Correbidia terminalis</i>	8	24	15	8	5	1	0	1	0	0	62	Silent
<i>Correbia lycoides</i>	7	11	5	0	1	2	0	0	0	0	26	Silent
<i>Delphyre rubricincta</i>	11	8	2	5	0	0	0	0	1	0	27	Silent
<i>Calonotos tiburtus</i>	6	31	3	0	1	0	0	0	0	0	41	Silent
<i>C. metallicus</i>	2	8	1	2	0	0	0	0	0	0	13	Silent
<i>Macrocneme</i> spp.	23	22	2	2	0	1	1	0	0	0	51	Silent
<i>Homoeocera stictosoma</i>	0	0	1	7	2	4	3	1	0	0	18	Silent

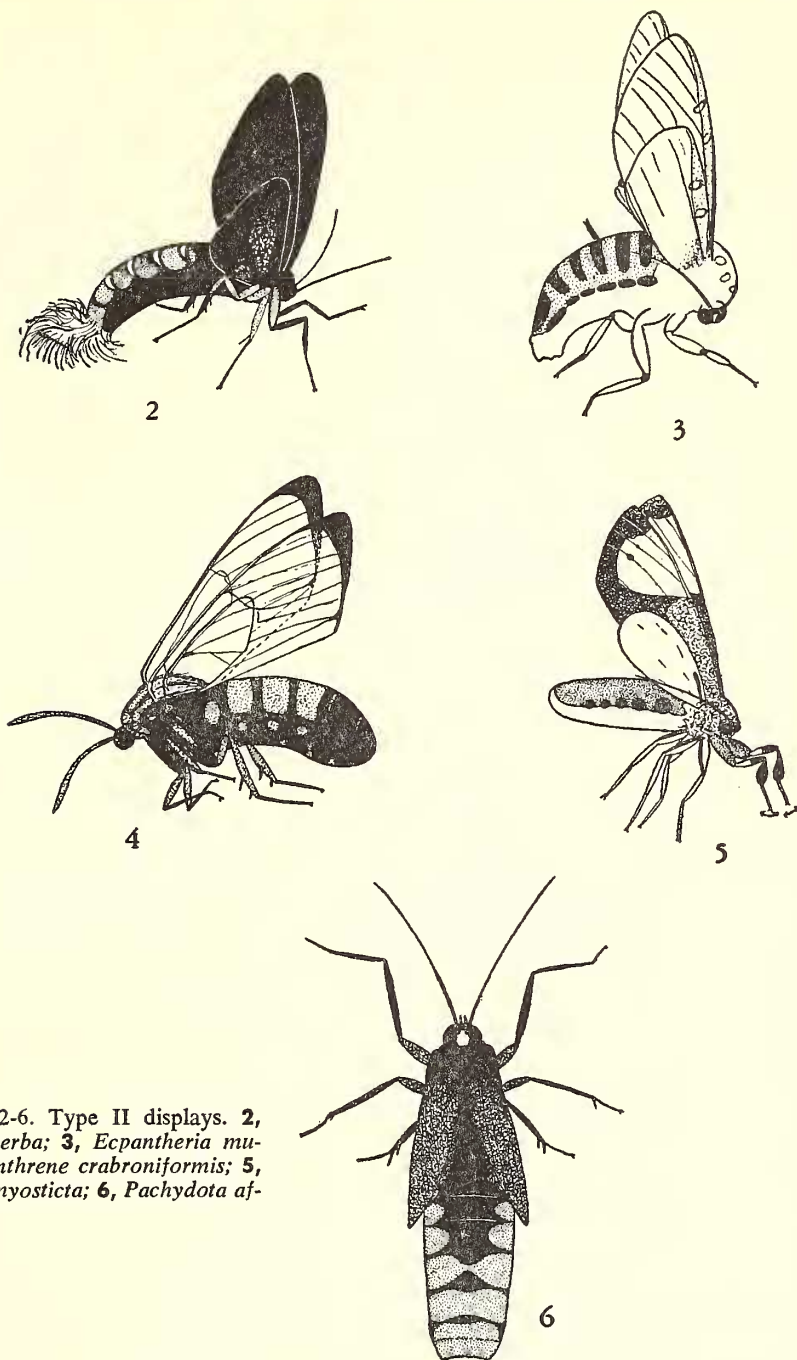
*Hair Tufts*.—Some ctenuchids (e.g., *Eucereon decora*) have a series of lateral hair tufts on the anterior part of the abdomen, which is concealed

at rest, and only erected during display. Display is of Type II, and the erected hair tufts are therefore readily visible to a predator. Some



TEXT-FIG. 1. a. *Calonotos craneae*, reflex immobilization, female. b. *Macrocneme thyra intacta*, male. Reflex immobilization, with slight extrusion of the genitalia.



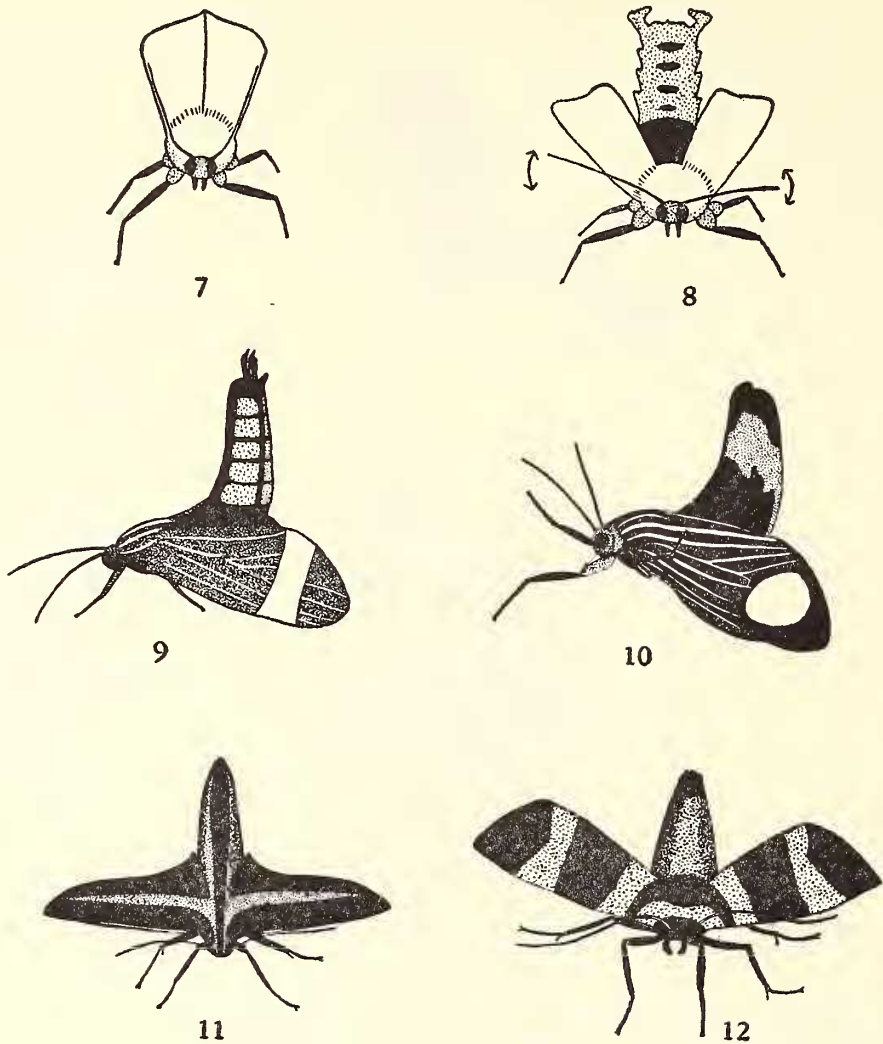


TEXT-FIGS. 2-6. Type II displays. **2**, *Baritius superba*; **3**, *Ecpantheria muzina*; **4**, *Isanthrene crabroniformis*; **5**, *Bertholdia myosticta*; **6**, *Pachydota affinis*.

*Eucereon* spp. and related genera have red or orange cervical hair tufts which are only exposed when the moths are handled.

(iii) *Release of Materials from the Ventral Valve*.—The males of certain ctenuchids possess a specialized ventral abdominal structure, the ventral valve, which in some species encloses

a yellow or whitish secreted product. In only one of the species observed in this study has any directly protective function been noted for this material, though it may assist in rendering the moths unpalatable. In *Homeocera stictosoma*, light restraint of the insect elicits reflex immobilization, and the instant release of the accumu-



TEXT-FIGS. 7-12. Type III displays. 7, *Automolis elissoides* at rest; 8, *A. elissoides* displaying; 9, *A. rutila*; 10, *A. chionoplaga*; 11, *A. taeniata*; 12, *A. tegyra*.

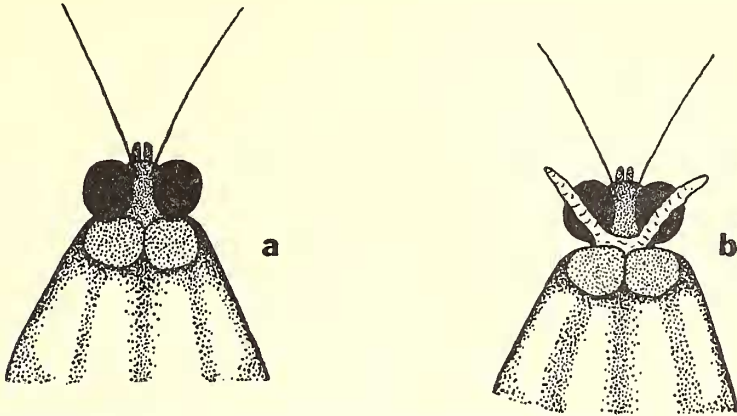
lated secretion, in the form of a light white flocculent material composed of fine friable fibres which rapidly envelop the animal, and which have a faint but definite phenolic odor. They are dispersed when the insect flies away. The material is not replenished after it has been used, and the ventral valves of animals which have released it remain empty until they die.

(iv) *Reflex Bleeding*.—In a great many species reflex immobilization is accompanied by reflex bleeding from the joints and prothorax. It is particularly copious in *Histaeta cepheus* and *Amastus rumina*.

(v) *Specialized Secretions*.—Several European arctiids are known to possess specialized defensive secretions which are emitted from

glands in the prothorax (Bisset, Frazer, Rothschild & Schachter, 1960). In one case (*Arctia caca* (L.)), the secretions have been shown to contain an unusual higher alkyl choline ester, probably  $\beta$ - $\beta$ -dimethylacrylylcholine, or a near derivative (Bisset *et al.*, *loc. cit.*). It is likely that some of the species under consideration may possess such defensive mechanisms, but they were not specifically searched for in this study.

(vi) *Odors*.—Most arctiids and ctenuchids which are definitely distasteful have a noticeably unpleasant, musty odor to the human observer, and they are often rejected by *Cebus* in test situations after being smelled but not tasted. These odors are absent or less noticeable in



TEXT-FIG. 13. a. & b. Cervical region of unidentified ctenuchine near *Eucereon*, to show extrusible lemon-yellow processes.

species which have proved palatable to both *Cebus* and *Oedipomidas* (e.g., *Melese laodamia* and *M. asana*). Odor is not, however, a necessary concomitant of unpalatability, for *Bertholdia myosticta*, which were consistently rejected by chickens, do not possess a strong smell.

*Delphyre rubricincta*, which performs a Type II display exhibiting a black and crimson banded abdomen, simultaneously releases a foul odor of short persistence. No visible droplets of fluid have been seen to accompany it, and its origin is consequently for the present unknown. This odor somewhat resembles that of the alarm substance of the large neotropical ants of the genus *Paraponera*. Specimens of *Gymnelia salvini* have a faint but similar odor.

(vii) *Frothing*.—*Belemniastis troetschi* and *Autochloris jansonis* froth vigorously from the thorax when they are handled. Many pericopids produce froth and so do African members of the genus *Rhodogastris* (Arctiidae) (Carpenter, 1938).

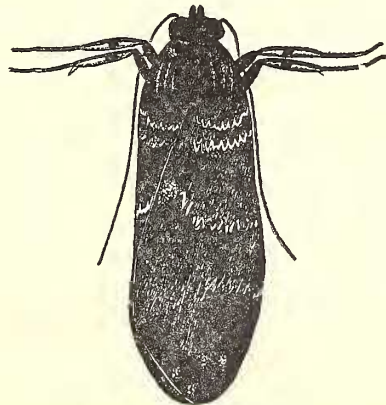
(viii) *Other Specialized Components*.—Although the general forms of the displays are remarkably stereotyped, the minor components are often modified. For example, species of *Baritius* tend to retain their hold on the substrate while performing a Type II display, and *B. haemorrhoides* and *B. superba* back away from the disturbing stimulus, following a semicircular path. *Bertholdia* spp. place the first pair of legs in a specialized posture and quiver them rapidly (Fig. 5); similar specialized leg postures are also found in *Melese asana* and *M. incerta*, and in *Halysidota underwoodi*.

The ctenuchid *Sarosa innotata* accompanies an otherwise normal reflex immobilization with vertical bobbing movements of the abdomen, which is yellow with a black tip; the significance of this behavior pattern is obscure, and similarly

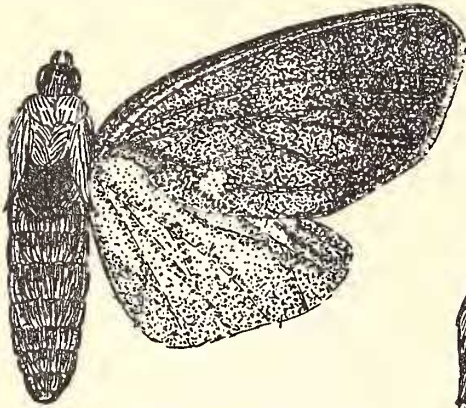
marked species of *Cosmosoma* (e.g. *C. hercyna hercynacula*) do not possess it.

A single specimen of an unidentified ctenuchine near *Eucereon* from Santa Clara extruded a pair of flabby lemon-yellow processes from the cervical region when touched (Text-fig. 13). No perceptible odor was associated with them. *E. leria* and *E. tarona* bent their heads forward to expose crimson hair tufts in the same region.

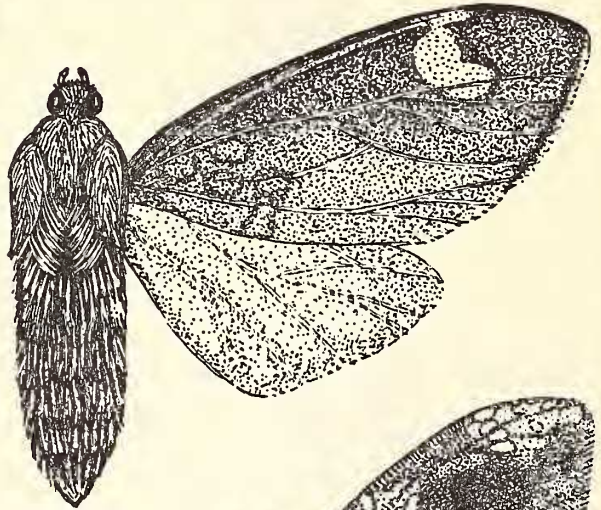
Perhaps the majority of ctenuchids show some degree of mimicry, hymenopterous and dipterous insects being the most usual models. A general account is given in the various sections of Seitz's "Macrolepidoptera of the World" dealing with the family. Although the flight patterns of these mimetic species often closely resemble those of the various models, their resting behavior is relatively little specialized; the more extreme wasp-mimics, however, (e.g., *Pterygopterus leucomela*) walk with the jerky movements of their models, and may even palpate the surface of the ground with their antennae in a wasp-



TEXT-FIG. 14. The resting posture of *Eucereon obscurum*.



TEXT-FIG. 15



TEXT-FIG. 16



TEXT-FIG. 17

TEXT FIGS. 15-17. Cryptic and pro-cryptic species. **15**, *Melese incerta*; **16**, *M. laodamia*; **17**, *Ochrodota pronapides*.

like manner. An account of some ctenuchid flight adaptations is given by Beebe & Kenedy (1957).

VII. *Cryptic Coloration*.—Although several genera have an inconspicuous appearance, perhaps equivalent to “generalized cryptic coloration” in the saturniids (Blest, 1957) (e.g., *Melese*, *Bertholdia*, *Elysius*, *Ammalo*) (Text-figs. 15 and 16), very few appear to have specialized pro-cryptic coloration. The exceptions, which have been shown to be palatable (*Ochrodota pronapides* (Text-fig. 17), *Amoxia pyga*, *Melese chiriquensis*), are also striking for their fragility; this correlation between pro-crypsis and fragility can probably be explained in terms of natural selection, and requires more extensive study (Blest, 1963a).

#### 4. NOTES ON INDIVIDUAL GENERA

Although a list of the species and their behavior is given in Table I, certain genera deserve special discussion.

#### I. *Automolis*.

Forbes (1939) considers that this genus is not homogeneous, and it has been split into a number of species-groups. Its protective behavior is of two kinds: reflex immobilization, and Type III display. Either may be accompanied by sound production, the threshold for which is lowest in those species showing reflex immobilization only, and highest in *A. taeniata*, only one of some two dozen specimens producing an auditory signal. Since *A. taeniata* maintains its display particularly vigorously, it would appear that this relation may be merely a matter of the occlusion of sound production by the competing display reflex.

Despite the uniformity of the Type III displays, the visual patterns which they exhibit vary widely (Text-figs. 7-12). *A. dilutus* apparently mimics an implausibly large lampyrid

beetle and does not display. Tactile or visual stimuli cause it to fall to the ground, and the related *A. reducta* behaves in the same way.

All members of the genus tested showed some degree of unpalatability; some species (e.g., *A. sicilia*, *A. vitrea*) were occasionally accepted by *Cebus*, although the majority of individuals were rejected. Most species were consistently rejected (*A. metallica*, *A. diluta*, *A. crithis*, *A. elissa*, *A. elissoides*), and survived investigation and rejection by *Cebus* on the majority of occasions. *A. taeniata* proved highly distasteful to domestic fowl, and individual birds rapidly learned to ignore them.

## II. *Cissura*.

This genus was represented by one species only, *C. plumbeus* on Barro Colorado. It is notable for the coupling of reflex immobilization to sound production at very high threshold, the signals consisting of a brief train of short squeaks. The coloration is aposematic, and comprises longitudinal carmine stripes on a dark slate-gray ground. This was the only species which all the *Cebus* in the colony learned to ignore on sight, and of which every individual survived investigation during the early encounters.

## III. *Robinsonia*.

All members of this genus have Type III displays, and all produce sounds. Two of the species (*R. deiopea* and *R. sanea*), (Text-figs. 18 & 19), have uniformly pale yellow abdomens and rest in the normal arctiid position, with the abdomen concealed by the folded wings. *R. flavomarginata* can be found resting on the undersides of the

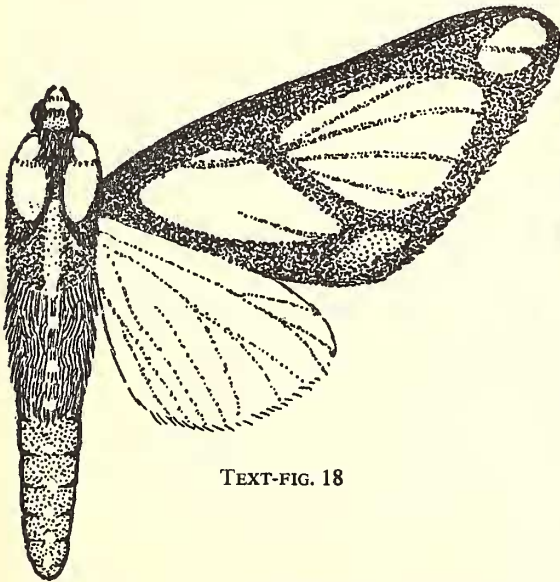
leaves of low second-growth vegetation in the forest; this and the similar *R. variegata* show convergence towards the smaller pericopids which may be found in the same habitat, particularly in the concentration of dark pigmentation along the veins of the forewings; they share the pericopid habit of resting with the brightly colored abdomen exposed.

## IV. *Eucereon*, *Delphyre*, *Heliura*, *Hyaleucera gigantea*.

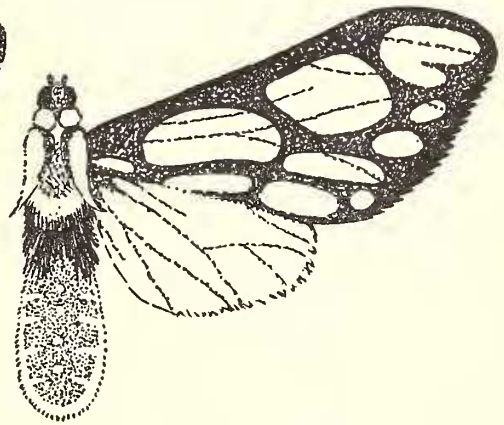
All the species of this group which have been tested have proved unpalatable. The 27 species from Barro Colorado and Santa Clara assort themselves into the following groups on the basis of their wing patterns; 24 belong to *Eucereon*, to which three other genera are convergent.

This grouping omits *Delphyre atava*, which resembles an *Episcepsis*, and *D. aurorina*, *Heliura banoca* and *H. rhodophila*, which neither resemble each other nor any of the main groups of *Eucereon*. Group II is more diversified than the others, and no account is taken of the numerous species of *Eucereon* found in Trinidad.

Each of these types of pattern is distinct, and the members of each group are closely similar to each other. The species in most cases are adequately illustrated by Seitz. The distribution of these species between Santa Clara and Barro Colorado suggests the following conclusions: (i) In most cases each group can be treated as two small subgroups of similar sympatric species, with little overlap. (ii) Each such subgroup functions as a potential Müllerian assemblage. (iii) There is a rather striking pattern of replacement within each group. Thus, in Group I,



TEXT-FIG. 18



TEXT-FIG. 19

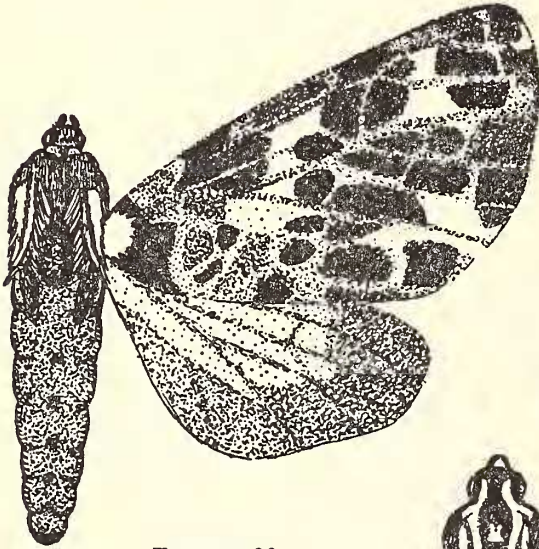
TEXT-FIGS. 18 & 19. *Robinsonia*. 18, *R. deiopea*; 19, *R. sanea*.

Group I	Group II	Group III	Group IV
<i>leria</i> (S)	<i>aeolum</i> (B)	<i>zamorae</i> (B)	<i>atrigutta</i> (BS)
<i>tarona</i> (B)	<i>aoris</i> (B)	<i>flavicaput</i> (BS)	<i>formosa</i> (S)
(Text-figs. 20, 21).	<i>pseudarchias</i> (B)	<i>scyton</i> (B)	<i>tigrata</i> (S)
	<i>latefascia</i> (B)	<i>decora</i> (S)	(Text-figs. 26, 27).
	<i>myrtusa</i> (S)	<i>xanthura</i> (B)	
	<i>rosa</i> (B)	<i>rogersi</i> (S)	
	<i>Heliura ballia</i> (B)	(Text-figs. 24, 25).	
	<i>Delphyre rubricincta</i> (B)		
	(Text-figs. 22, 23).		
Group V	Group VI	Group VII	Group VIII
<i>striata</i> (S)	<i>obscurum</i> (BS)	<i>zephyrum</i> (B)	<i>maia</i> (B)
<i>costulata</i> (S)	<i>Hyaleucera gigantea</i> (BS)		(Text-fig. 29)
<i>phaeoprocta</i> (B)	(Text-fig. 14).		
<i>intranotata</i> (B)			
(Text-fig. 28).			

B = Barro Colorado; S = Santa Clara.

*tarona* on Barro Colorado is replaced in Santa Clara by the very closely similar *leria*; in Group V, *phaeoprocta* and *intranotata* by *costulata* and *striata*. The close similarity between the patterns and coloring found in the two habitats in these distasteful species is in striking contrast to those

of the predominantly procryptic families such as the Lasiocampidae and Noctuidae, where the wealth of lichens, mosses and epiphytes at the higher altitude has provoked the evolution of patterns and coloration distinct from the forms prevalent on Barro Colorado (Blest, 1963a).

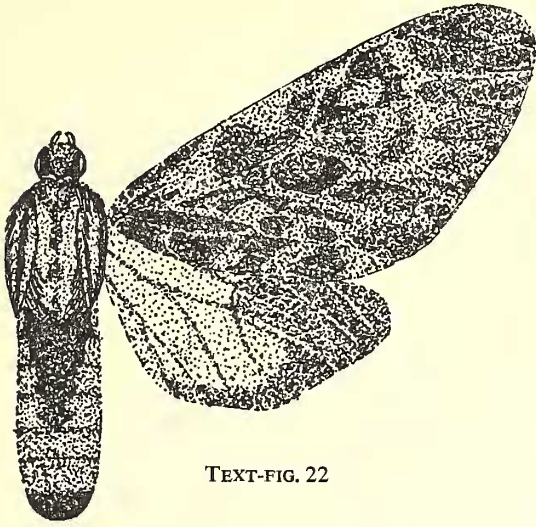


TEXT-FIG. 20

TEXT FIGS. 20 & 21. *Eucereon*, Group I.  
20, *E. tarona*; 21, *E. leria*.



TEXT-FIG. 21

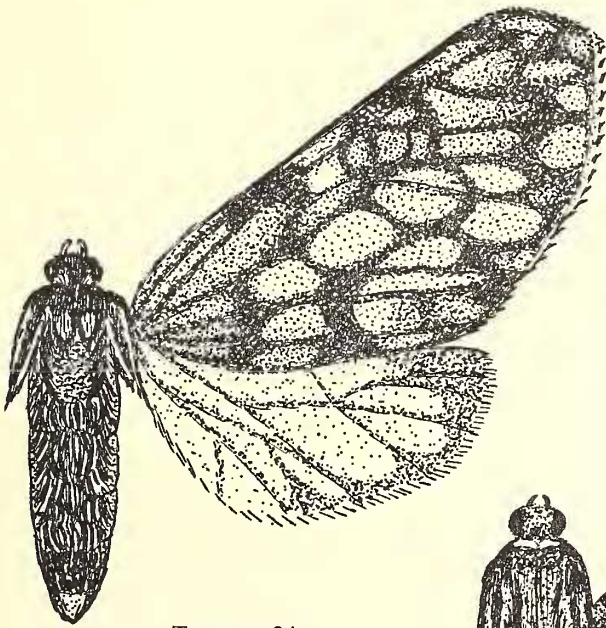


TEXT-FIG. 22



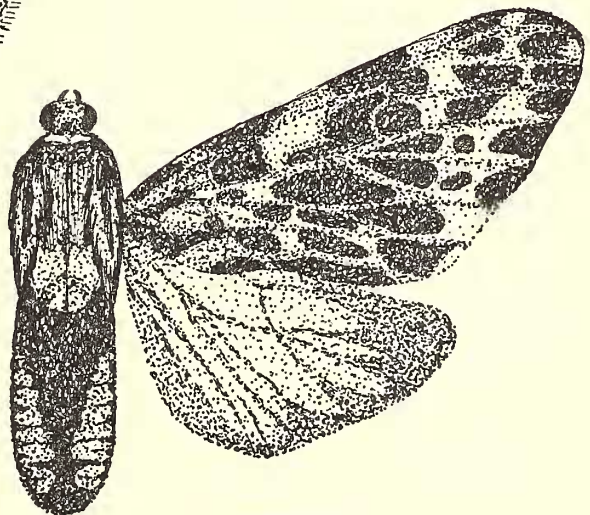
TEXT-FIG. 23

TEXT-FIGS. 22 & 23. *Eucereon*, Group II. 22, *E. latefascia*; 23, *Heliura balia*.

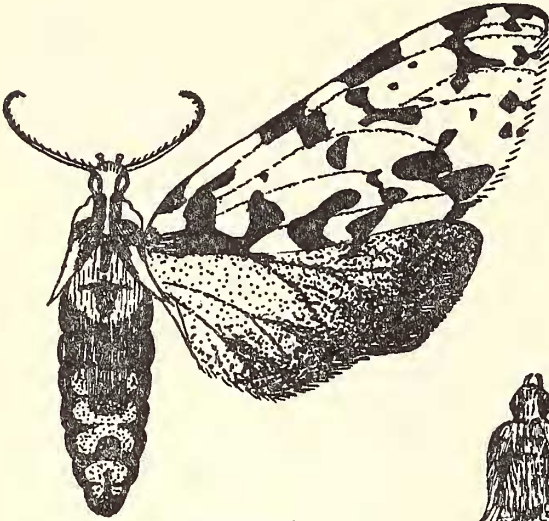


TEXT-FIG. 24

TEXT FIGS. 24 & 25. *Eucereon*, Group III. 24, *E. flavicaput*; 25, *E. rogersi*.

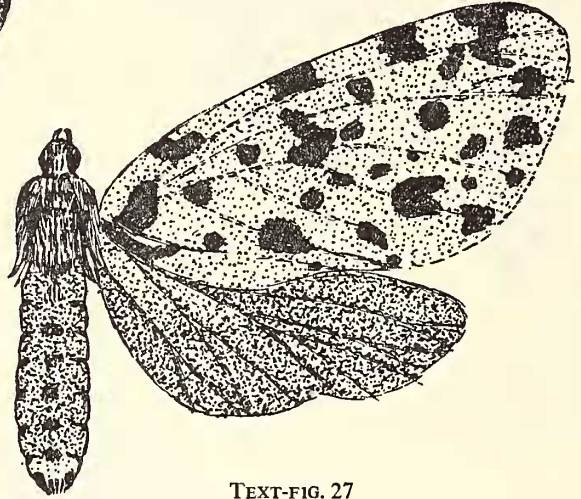


TEXT-FIG. 25



TEXT-FIG. 26

TEXT-FIGS. 26 & 27. *Eucereon*, Group IV. **26**, *E. tigrata*; **27**, *E. formosa*.



TEXT-FIG. 27

It is possible that the existence of similar groups of "equivalent" species in the two areas is merely a function of the niches available to the larvae, and of the stability of the color patterns within the groups. However, there still remains the possibility that the distribution of aposematic patterns within populations of sympatric species is determined by some feature of predator behavior which has not yet been appreciated. For example, Van der Vecht (1961) has provided some support for regarding the action of local predator populations as selectively critical, in a study of the Indo-Australian wasps of the genera *Eumenes*, *Pareumenes* and *Pseudeumenes*. In this case, *Eumenes flavopictus*, extending from southern India to New Guinea, is mimicked by species of *Pseudeumenes* and *Pareumenes*. All three genera show parallel variation throughout their range, and form in each locality where they simultaneously occur a distinctively patterned Müllerian assemblage. The size of the departure from the pattern of the mainland *Eumenes* population relates directly to the degree of isolation of the divergent populations. It seems necessary to assume that in each isolate specific local patterns of predation have stabilized the dominant species (*Eumenes flavopictus*) and have caused convergence with the other two

genera. This interpretation holds whether or not genetic drift is invoked to explain the initial divergence between the island and the mainland populations.

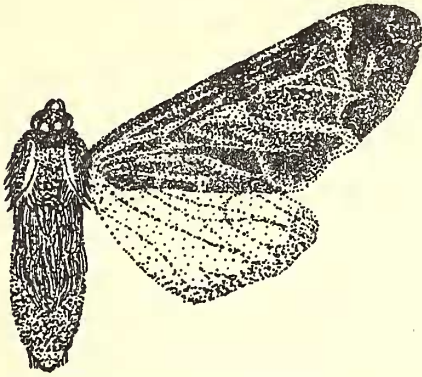
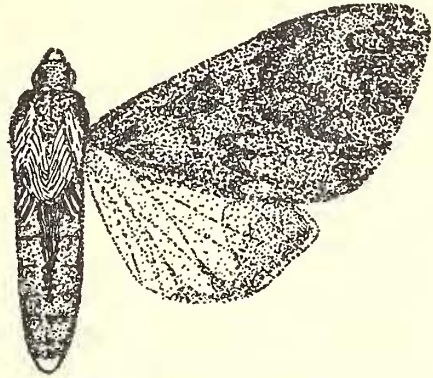
#### V. *Macrocneme*, *Calonotos*.

In both these ctenuchid genera, the male genital apparatus has been elaborated in certain species to provide a warning signal. *Macrocneme thyra intacta* and *M. adonis* belong to a division of the genus in which the male ventral valve is large and bifid. The whole genital apparatus, which is bright yellow in life, is extruded during reflex immobilization. In the remaining species it remains retracted, and the valves are small and usually asymmetrical (Forbes, 1939). A similar trend is found in *Calonotos*. Males of *C. craneae* possess supernumerary genital processes and instantly extrude the genital apparatus when restrained. It is feebly sclerotized, bright yellow, and has a fleshy appearance in life. *C. tiburtus* and *C. metallica* lack the extra process; the apparatus is normally sclerotized, brown, and is not spontaneously extruded during handling.

#### 5. SYSTEMATIC CONSIDERATIONS

Little can be concluded from the distribution



TEXT-FIG. 28. *Eucereon*, Group V. *E. costulata*.TEXT-FIG. 29. *Eucereon*, Group VIII. *E. maia*.

of display behavior within the two families. Within the Arctiidae, it can be said that no arctiine possesses a Type III display, which is only found in certain Phaegopterinae (*Automolis*, *Robinsonia* spp.). Type II displays are found in both subfamilies, and in certain ctenuchids. In general, the imprecise morphological division between the ctenuchids and arctiids, most evident in such transitional genera as *Belemnina*, *Belemniasis* and *Diospyge*, is paralleled by their behavior. Such ctenuchines as *Delphyre* and *Eucereon* spp. differ little in their behavior (reflex immobilization or Type II static displays) from arctiids such as *Agoraea* and *Ecpantheria* spp. The abandonment of the characteristic arctiid displays and resting and reflex immobilization postures follows the adoption by the ctenuchids of varying degrees of mimicry of non-lepidopterous insects, and reduced wing-scaling.

#### 6. RELATIONS BETWEEN ENVIRONMENTAL TEMPERATURE AND DISPLAY BEHAVIOR

It is already clear that the persistence of static displays shows some relationship to environmental temperature. The ambient diurnal temperature on Barro Colorado fluctuates around 27° C at a height of 55 ft. in the forest shade (Allee, 1926), and may reach 34° C during the day. This latter temperature is nearing that of working lepidopterous muscle as measured by Krogh & Zeuthen (1941) for temperate nymphalids and sphingids and by Dorsett (1962) for tropical sphingids. It follows, and observation confirms, that on Barro Colorado only small periods of shivering need precede fully competent flight. Indeed, large and heavy sphingids and saturniids often make successful escape flights without shivering at all. It might be argued, then, that for a species only moderately unpalatable and not physically resilient, selection might well favor escape flights over a protracted display. In

fact, this appears to be the case. The static displays of the Barro Colorado arctiids and ctenuchids are transient, and are only held for periods of seconds; so much so that they have proved difficult to photograph.

At Santa Clara, however, at an altitude of 4,000 ft., the temperatures are lower. Apparently in correspondence, displays and reflex immobilization are long-persisting. *Automolis taeniata* and *A. tegyra* maintained Type III displays invariably for periods of seconds, and sometimes for minutes. On Barro Colorado, *A. tegyra*, and *A. metallica* which belongs to the same species-group as *A. taeniata*, both gave only transient displays. At Volcán itself, *Halysidota underwoodi* gave a lengthy display which added specialized leg postures to reflex immobilization. At Barro Colorado, *H. interlineata*, closely related to it, assumed reflex immobilization without leg components for no more than brief periods.

The evidence from arctiid and ctenuchid displays alone does not allow a certain distinction between the effects of natural selection for a display length adjusted to the diurnal ambient temperature, and the mere effect of immediate temperature upon the physiological and behavioral responses of the individual moths. Controlled experiments were not possible, but chilling *Automolis* on Barro Colorado did not seem to lengthen their displays by a substantial amount. The best evidence favoring the first alternative comes from the hemileucine saturniids; there, the palatable forms in general bear eyespot patterns, and either display them statically, or perform rhythmic displays. With the exception of *Automeris janus*, which occurs at a wide range of altitudes, and rare individuals of *A. tridens* and *A. junonia*, none of the Barro Colorado *Automeris* with simple static displays (8 species) perform rhythmic components,

while of the Santa Clara *Automeris* which were seen as adults, two (*A. nyctimane* and *A. subpicta*) had low-threshold rhythmic displays, while one (*A. montezuma*) had rhythmic leg components. *A. nyctimane*, received in England as pupae from Bogotá, Colombia (8,000 ft.), also had low-threshold rhythmic displays. All were well sustained, in contrast to the transient displays of the Barro Colorado *Automeris*.

In addition, two species, *A. junonia* and *A. tridens*, perform brief static displays on Barro Colorado, and chilling fails to elicit a rhythmic performance. In the Arima valley of Trinidad (diurnal temperature fluctuating around 25° C) a proportion of individuals of both species perform rhythmic displays, as does the related *A. liberia*. The species whose displays are characteristically of low threshold (those of the *A. nyctimane* group) are typically either montane, or found at the extremes of the range of the genus, in southern Brazil and Argentina, and in Mexico. A detailed study of their distribution in terms of their environmental temperatures and display performance would be of great interest.

#### 7. THE GENERAL ADAPTIVENESS OF DISPLAY AND ESCAPE BEHAVIOR

Probably the most important predators of these small moths are insectivorous birds, notably the numerous species of tropical flycatcher (Tyrannidae) and bats, though nothing is known about the patterns of predation prevailing in the forest canopy. It is likely that birds discriminate more carefully in their choice of prey than the captive monkeys used in these observations, if only for the reason that monkeys caged in groups are in a competitive situation in which prey is eaten to assert dominance, or even to please the experimenter, as well as to satisfy hunger. For example, Silver-beaked Tanagers rejected *Melese laodamia*<sup>3</sup> while the two primates accepted it, and domestic fowl took the equivalent species (*M. russata*) at Santa Clara. For these reasons it is remarkable that so many of the species achieved almost complete protection against the caged *Cebus*. The small number of experimental predators and the erratic appearance of any one species of moth precluded formal palatability tests of the kind so elegantly used by Brower (1958, 1960); tests with *Cebus* were confined to some dozen presentations to the colony in each day, in which no more than eight arctiids were presented, the remaining species being palatable sphingids, noctuids and geometrids. The moths were pushed through the wire, and in most

cases the monkeys took them directly in their hands.

From the observations which resulted, it appears that there are two rather distinct ways in which an unpalatable species may survive investigation by an inexperienced monkey. *Cebus* pick up small prey in their hands, and smell it before biting it. Arctiids and ctenuchids are usually rejected at this stage. An actively struggling prey is usually picked to pieces, however, even if it is not subsequently eaten; the rejection tends to be followed by manual investigation which is sufficiently vigorous to elicit struggling from those saturniids which have static displays. Arctiids, however, remain passive throughout this phase, and are ultimately dropped. In nature they would fall some 30-90 ft. from the forest canopy to the ground. Even in cage conditions they succeed in creeping away without exciting further attention. Correlated with this behavior is an outstandingly tough and leathery consistency. Such moths (*e.g.*, *Automolis metallica* and related species) will suffer quite violent investigation without lethal injury.

The alternative method of escape exploits the fact that a monkey when holding a passive prey eventually opens its hands to look at it; species such as *Eucereon* and the euchromiine mimics of Hymenoptera and Diptera terminate their reflex immobilization with instant flight as soon as tactile restraint is removed. *Eucereon aoris* and small *Macrocne* repeatedly eluded *Cebus* in this way.

It is likely that these two escape mechanisms may succeed against most small primates, and perhaps avian predators as well.

#### 8. DISCUSSION

The main problem raised by these observations may be simply stated: the arctiids and ctenuchids consist of predominantly distasteful insects. So unpalatable are they that most species are rejected even by caged colonies of *Cebus*. If it is assumed that predators in nature must learn to avoid distasteful species, and that those which search visually learn best bold aposematic patterns of a conventional kind (Cott, 1949), then it follows that selection should tend to promote Müllerian convergence in any one taxonomic group of distasteful animals, given certain simplifying conditions in the ecological situation (Blest, 1963a). These conditions consist, in the main, of the mere absence of various sources of constraint. Convergence, for example, might be prevented were the animals to use visual signals for sexual recognition, in which case selection for character divergence as an isolating

<sup>3</sup>Tests with Silver-beaked Tanagers were conducted by Mr. T. S. Collett and Mr. C. T. Collins in Trinidad.

mechanism (Brown & Wilson, 1956) should tend to sustain the opposite change in any one ecological assembly. Interactions between sexual and mimetic demands of just this character have been described by Stride (1956, 1957). Associations between specialized procrystic coloration and highly evolved habitat-selection could also bring about the same result. In the present case neither of these restraints would appear to operate. The majority of species in both families are highly and efficiently distasteful; they are not, in general, cryptic at rest, and since they are fully nocturnal (with the exception of the Ctenuchinae and some Euchromiinae), there is little likelihood that their courtship involves visual signals. Yet the course of evolution within these families seems often to have involved the maximum divergence of color patterns, even within genera. This is particularly striking in the case of the *Automolis* spp. illustrated in Text-figs. 7-12; all have Type III displays, and some, at least, are unquestionably closely related, (*A. chionoplaga*, *A. priscilla* and *A. rutila*, for example), yet the overall patterns are very distinct. Of the 16 *Automolis* found on Barro Colorado, only three (*A. elissa*, *A. elissoides* and *A. salma*) are closely similar to each other. On the other hand, there are apparently convergences across genera (some *Episcepsis*, *Delphyre atava* and *Aclytia ventralis* are much alike) or even families (e.g., the arctiid *Automolis rutila* and part of the ctenuchine genus *Aclytia*), and even participation in outside mimetic complexes (for example, wasp-mimicry, carried to such extremes as in the ctenuchid genera *Pseudosphex* (Beebe & Kenedy, 1957), and *Pterygopterus*, and the association of *Correbia* and *Correbioides* spp. (Ctenuchidae) with lycid beetles and their mimics; a North American lycid mimetic assembly is discussed in detail by Linsley, Eisner & Klots (1961). Finally, there are those genera which have maintained a close internal similarity; many of the numerous species of *Macrocneme* can only be distinguished reliably by genital characters, and the large distasteful genera *Eucreon* and *Episcepsis* each contains numerous closely similar species.

These discrepancies between simple prediction and fact need explanation; at the least they suggest the hazards of facile evolutionary speculation. Although the confusing and contradictory situation which is presented could be explained on the assumption that much of the adult coloration results from pleiotropic genes whose adaptive significance lies in other spheres, it is preferable to assume that the adult patterning is adaptive. Given this premise, two types of problem are presented:

(i) The case represented by *Automolis*, where

intrageneric divergence has been achieved without, in general, any close Müllerian resemblance to co-existent species outside the divergent group.

(ii) The case presented by many ctenuchine and euchromiine species where divergence has implemented Müllerian resemblances to non-lepidopterous insects.

These trends can only be understood in relation to the behavior of predator populations, and the type of information that is needed for their analysis is almost wholly lacking. The selection pressures are perhaps most likely to relate to the distribution of feeding habits within the assemblies of predator species. Research to date has been largely concerned to demonstrate that the learning and discriminatory capacities of single predator species are a sufficient explanation of the mimetic detail which is actually found in nature. It is well known that those highly aposematic and distasteful species which have been studied prove to be the victims of one or more natural predators which are undeterred by devices which are effective against more fastidious enemies (Cott, 1949). For example, whereas highly distasteful hemileucine saturniids are rejected consistently by marmosets, the less fastidious, and, in caged colonies, more highly motivated *Cebus* will take them, and quite soon learn to rub off the distasteful vestiture of hairs and scales (Blest, 1963b, and unpublished data). It has been correctly recognized that the existence of such predators, immune to the protective mechanisms of particular species, does not invalidate the general evolutionary argument. But the merely partial efficiency of these adaptations has not been seen as an active selective force in its own right.

Avian predators, so far as is known, learn to search for their prey within ecological limits doubtless determined by inborn releasing mechanisms, and they must also learn to avoid distasteful species. In an inexperienced predator population, the discovery and consumption of a palatable prey increases the probability that more prey of the same kind will be taken (de Ruiter, 1956; Blest, 1963b), and, if Tinbergen's (1960) hypothesis of "specific search images" retained over relatively long periods by the members of predator populations proves valid (Gibb, 1962), the behavior of the predator populations themselves is altered by experience. It would follow, then, that the existence of specific search images could provide a source of selection pressures promoting divergence within related aposematic forms, if there were even one species of predator for whom the group as a whole proved palatable. For the greater the population density of visually similar forms, the more rapidly will a specific

search image directed to them be set up; and this adaptively undesirable consequence of Müllerian resemblance will be attenuated if the similarities are broken down and replaced by divergences in the course of evolution. In fact, the situation would necessarily impose simple direct selection for divergent forms, which might or might not be balanced by the factors promoting Müllerian convergence. The plausibility of this hypothesis can only be assessed when much more is known about the pattern of avian predation in tropical forest. In particular, the relatively narrow ecological niches which are said to be characteristic of tropical birds (MacArthur & MacArthur, 1961; Klopfer & MacArthur, 1961; Klopfer, 1962) may prove to have special selective consequences for insects with spatial distributions which are complex in relation to those of their potential predators.

In contrast to what has been claimed for the saturniids (Blest, 1957), there is no clear derivation for the display behavior of these two families. Although there are rhythmic displays of the type which have been assumed to be transitional between flight behavior and static displays (Blest, 1957), there is no evidence of intermediate types; all the displays are static save for the leg-quivering movements found in some *Bertholdia*, etc., and a few other specialized components, and wing-waving appears only as an accompaniment of walking. The evolutionary origins of the static displays are consequently obscure. Rhythmic displays in which the wings are slowly raised and lowered without locomotion are performed by the North American *Diacrisia virgo*, but nothing can be said about the relationship which they may bear to the present tropical behavior patterns. Nor, as was hoped when the study was started, is the origin and precise function of sound production suggested by comparative study. All that contemporary species seem able to demonstrate is that when unpalatability has reached a certain degree, the capacity to produce ultrasonic sounds is lost, presumably because it confers no further advantage. At present, too little is known about the treatment of unpalatable prey by bats for their significance to be assessed.

#### 9. SUMMARY

1. The protective display behavior of 183 New World species of arctiid and ctenuchid moth from Trinidad and Panama is summarized, and compared with that of the Saturniidae. Their displays are characterized by the independent evolution of a large variety of "specialized" devices, sometimes developed uniquely, but often showing intergeneric con-

vergence. All but a few displays are static and there are virtually no rhythmic components. The most advanced forms seem to rely upon "reflex immobilization" as a defence.

2. Most members of the two groups possess tymbal organs on the metathorax, but only a minority of species use them to produce ultrasonic signals when handled, and the ability to do so is lost in the advanced ctenuchids, although some ctenuchines transitional between the two families (e.g., *Eucereon*, *Episcepsis*) readily emit sounds. There is no correlation between the mode of protective coloration and the tactile threshold for sound-production, save that in the more palatable phaegopterine arctiids (e.g., *Melese*, *Bertholdia* and *Ochrodota* spp.) the threshold for sound-production is lower than in those which are more distasteful (e.g., *Automolis*, *Robinsonia* and *Cissura* spp.).
3. The possible role of environmental diurnal temperature in determining the course of the evolution of protective displays is discussed.
4. It is suggested that the families show less simple Müllerian convergence within genera than might be predicted from their almost uniform unpalatability. Reasons for this are discussed, with particular reference to L. Tinbergen's hypothesis of the "specific search images" of birds.

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